

Emergence of Lévy Walks in Systems of Interacting Individuals

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Recent experiments (G. Ariel, et al., Nature Comm. 6, 8396 (2015)) revealed an intriguing behaviour of swarming bacteria: they fundamentally change their collective motion from simple diffusion into a superdiffusive Lévy walk dynamics. We introduce a nonlinear non-Markovian persistent random walk model that explains the emergence of superdiffusive Lévy walks. We show that the alignment interaction between individuals can lead to the superdiffusive growth of the mean squared displacement and the power law distribution of run length with infinite variance. The main result is that the superdiffusive behaviour emerges as a nonlinear collective phenomenon, rather than due to the standard assumption of the power law distribution of run distances from the inception. At the same time, we find that the repulsion/collision effects lead to the density dependent exponential tempering of power law distributions. This qualitatively explains experimentally observed transition from superdiffusion to the diffusion of mussels as their density increases (M. de Jager et al., Proc. R. Soc. B 281, 20132605 (2014)).

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The ability of living cells and bacteria to maintain a collective migration is fundamental for many physiological and pathological processes. Self-organized and coordinated movement in living organisms occurs during wound repair, formation of biofilms, tumor invasion, morphogenesis, etc. [1, 2]. Cells and bacteria have a tendency to form the cohesive groups in which mutual interactions lead to a cooperative movement of the whole population. A particular example of such coordinated mass migration is a bacterial swarming, for which the movement of bacteria across a surface involves a formation of packed clusters (“swarms”) [3]. It has been found recently that the swarming bacteria can perform a Lévy walk [4]. The extraordinary feature of this movement is that the emergence of a superdiffusive motility is a result of the interactions between bacteria rather than the standard mechanism of controlling the individual frequency of tumbling. On the other hand, it was shown that the interactions between mussels lead to the transition from a superdiffusive Lévy walk to Brownian motion as the density of mussels increases [5]. The shift has been explained by the frequent collisions of organisms in a dense group.

These experiments clearly show that a *nonlinear Lévy walk model* is needed to explain the emergence of the power-law distribution of run distances and its tempering, since the standard models are based on the assumption of power-law distributed run distances from the inception [6–8]. Currently the model of emerging Lévy walk in systems of interacting individuals is not available, despite the number of publications on *Lévy movement* increased dramatically over the last decade [9–15]. One of the reasons for increasing interest in Lévy transport is that living organisms can use it to accelerate pattern formation which leads to improvement of individual fitness [16] and to optimize searching for sparse targets [17–20].

In this paper we propose a *nonlinear Lévy walk model* for which the superdiffusion is an emerging collective phenomenon. Motivated by the recent experiments [4, 5], we suggest the nonlinear persistent random walk model that

explain both (1) the emergence of superdiffusive motion of bacteria within a swarm and (2) the transition from superdiffusion to the standard Brownian motion through *nonlinear tempering* of the power law distribution of run distances. Modeling of the collective movement of individuals such as insect swarms, bird flocks, schools of fish, etc. has received a lot of attention in the last decades [21]. Apart from various Lagrangian (agent-based) models, many kinetic equations have been developed to describe interaction between individuals [22–26]. The crucial problem here is how to incorporate nonlinear interaction terms into non-Markovian random walks. To implement nonlinear effects we use the structural density approach together with a population density dependent turning rate. This method has been used by the authors for the analysis of subdiffusive random walks [27, 28] and Lévy walks [29]. We take into account the interactions between walkers on the mesoscopic level, at which the turning rate nonlocally depends on the mean field population density (nonlinear effect) and running time (non-Markovian effect).

Nonlinear Lévy walk model in 1-D. We consider proliferating individuals moving either left or right along one-dimensional space at a constant speed v . The generalization for high dimensions is outlined in the Supplementary Materials. Note that 1-D is enough to show that the superdiffusion can be an emerging nonlinear phenomenon. The key characteristic of such random movement is the turning rate \mathbb{T} , which defines moments when individuals change their direction of movements. We introduce the structural densities of individuals, $n_+(x, t, \tau)$ and $n_-(x, t, \tau)$, at location x and time t that move in the right direction (+) or the left direction (−) during running time τ since the last velocity switching [30]. The mean density of individuals moving right, (+), and left, (−), are defined as

$$\rho_{\pm}(x, t) = \int_0^{\infty} n_{\pm}(x, t, \tau) d\tau \quad (1)$$

and the total density $\rho(x, t) = \rho_+(x, t) + \rho_-(x, t)$.

To describe random movement of individuals with interactions, we assume that the rate \mathbb{T}_\pm at which individuals change their direction of motion depends not only on running time τ (non-Markovian effect) but also on the population densities ρ_+ and ρ_- (nonlinear effect):

$$\mathbb{T}_\pm(\tau, \rho_+, \rho_-) = \frac{\mu_\pm(\rho_+, \rho_-)}{\tau_0 + \tau} + \gamma_\pm(\rho_\mp), \quad (2)$$

where τ_0 is the time parameter. Inverse dependence of the first term in \mathbb{T}_\pm on the running time τ leads to a strong persistence of the random walk. The function $\mu_\pm(\rho_+, \rho_-)$ describes the alignment effects leading to cooperative movement of individuals in one direction. If, for example, an individual moves to the right and senses that neighbouring conspecifics move in the same direction then the likelihood of velocity switching decreases. The positive function $\gamma_\pm(\rho_\mp)$ takes into account the increase in the turning rate \mathbb{T}_\pm when the individuals avoid the collisions with those moving in the opposite direction. The external forces or chemotactic factors could be included analogously to systems with subdiffusion [31, 32]. Here we do not consider these effects.

In this paper we model the alignment among individuals by the function:

$$\mu_\pm(\rho_+, \rho_-) = \mu f(A_\pm), \quad (3)$$

with a non-local density dependent function $A_\pm(x, t)$:

$$A_\pm = a \int_{\mathbb{R}} e^{-\frac{|z|}{l_a}} [\alpha \rho_\pm(x+z, t) - \beta \rho_\mp(x+z, t)] dz. \quad (4)$$

Here μ is the exponent of a power law distribution in the absence of nonlinear interactions ($A_\pm = 0$), $f(x)$ is a positive and decreasing function of x with $f(0) = 1$, a is the strength of interactions and α, β are weight parameters. The decreasing function $f(A_\pm)$ indicates that the turning rate \mathbb{T}_\pm is reduced due to the presence of many conspecifics moving in the same direction. This negative dependence plays the central role in the transition from a standard random walk to a Lévy walk. The kernel $\exp(-|z|/l_a)$ describes a strength of alignment per unit density with the distance $|z|$, l_a is the characteristic length of the interaction zone. To illustrate the effect of alignment, let us consider the case $\alpha = \beta = 1$ for which the non-local function A_+ for right-moving individuals can be rewritten in terms of the flux $J = v(\rho_+ - \rho_-)$. We can write $A_+ = av^{-1} \int_{\mathbb{R}} \exp(-\frac{|z|}{l_a}) J(x+z, t) dz$, so the increase in the flux J leads to an increase of alignment effects and decrease of turning rate \mathbb{T}_+ . This indicates the emergence of nonlinear persistence which, together with running time persistence, can generate superdiffusive behaviour. Such modelling is in agreement with observation that the motion of swarming bacteria is mostly governed by the collective flow of the bacteria and surrounding fluids [4]. Note that the advantage of moving in a large group in the same direction is very similar to the

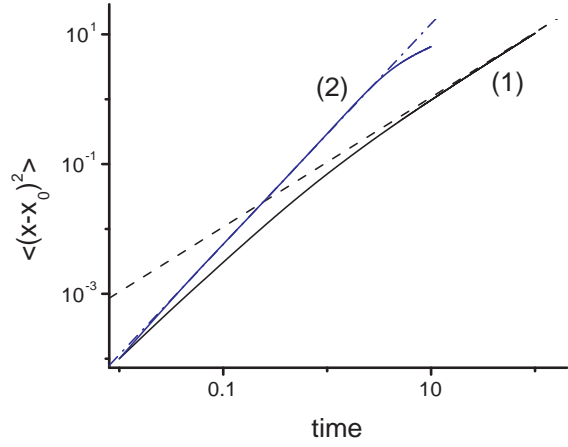


FIG. 1: Emergence of the Lévy walks when alignment dominates repulsion. The log-log plot of the MSD (curve (2)) displays the superdiffusive behavior with exponent 1.7 (dashed-dotted line). We have used $a = 1.5$, $\alpha = 1$, $\beta = 0$, and $r = 0$. Other parameters are $\mu = 3$, $\tau_0 = 0.1$, $v = 1$. Without interactions $a = 0$, $r = 0$ (curve (1)), the MSD grows linearly in the long time limit (dashed line has the slope 1).

“peloton” phenomenon in a road bicycle race. Similar non-local dependencies of the turning rate on the population density has been successfully used to describe the animal spatial group patterns and bacterial swarming in terms of the hyperbolic and kinetic models [22–26].

The second term $\gamma_\pm > 0$ in the turning rate \mathbb{T}_\pm , Eq. (2), describes the collision/repulsion effects. We assume the increase in the turning rate \mathbb{T}_\pm when individuals tend to avoid collisions with many conspecifics moving in the opposite direction:

$$\gamma_\pm(\rho_\mp) = r \int_0^\infty \exp\left(-\frac{z}{l_r}\right) \rho_\mp(x \pm z, t) dz, \quad (5)$$

where l_r is the effective repulsion size, and r is the strength of repulsion. The similar repulsion rate has been well used in the hyperbolic model [23] to obtain spatial patterns. In our non-Markovian model, the role of the collision/repulsion rate γ_\pm is drastically changed. This term is responsible for the shift from the superdiffusive Lévy walk to diffusion as the density increases [5].

The nonlinear equations for the structural densities $n_+(x, t, \tau)$ and $n_-(x, t, \tau)$ can be written as:

$$\frac{\partial n_\pm}{\partial t} \pm v \frac{\partial n_\pm}{\partial x} + \frac{\partial n_\pm}{\partial \tau} = -\mathbb{T}_\pm(\tau, \rho_+, \rho_-) n_\pm. \quad (6)$$

We use symmetrical initial conditions for which all individuals start to move with zero running time

$$n_\pm(x, 0, \tau) = \frac{\rho(x, 0)}{2} \delta(\tau). \quad (7)$$

Zero running time condition ($\tau = 0$) includes the prolif-

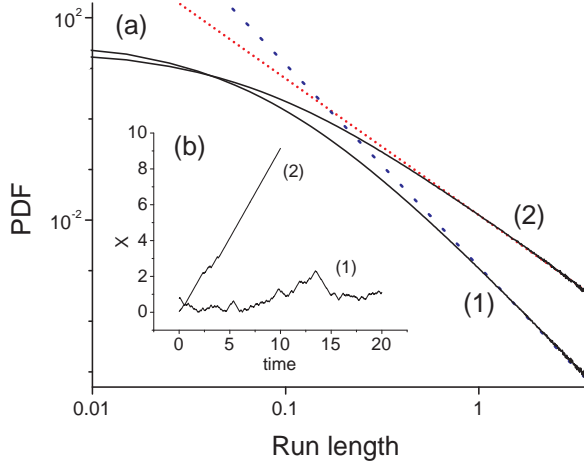


FIG. 2: (a) The run length PDF of the emerging Lévy walkers (curve (2)). Parameters are the same as in Fig. 1. The run length PDF is a power law with the slope -2.7 (the dashed line), that is the variance of the PDF is infinite. For non-interacting walkers the run length PDF is also a power law (curve (1)), but the slope is $-\mu - 1 = -4$ (the dotted line), so the variance is finite. (b) Typical trajectory of interacting Lévy walkers (curve (2), for better clarity we use $a = 2.5$) is very persistent unlike the Brownian-like trajectory for a walker without interactions (curve (1)).

eration of the individuals:

$$n_{\pm}(x, t, 0) = \int_0^t [\mathbb{T}_{\mp}(\tau, \rho_+, \rho_-) n_{\mp} + k(\rho) n_{\pm}] d\tau, \quad (8)$$

where $k(\rho)$ is the density dependent proliferation rate. This condition corresponds to the case when newborn individuals have zero running time. It is convenient to introduce the total turning rates defined as

$$i_{\pm}(x, t) = \int_0^t \mathbb{T}_{\pm}(\tau, \rho_+, \rho_-) n_{\pm}(x, t, \tau) d\tau. \quad (9)$$

Differentiating (1) with respect to time t together with (7) and (8) we derive the balance equations for the unstructured mean densities $\rho_+(x, t)$ and $\rho_-(x, t)$:

$$\frac{\partial \rho_{\pm}}{\partial t} \pm v \frac{\partial \rho_{\pm}}{\partial x} = -i_{\pm}(x, t) + i_{\mp}(x, t) + k(\rho) \rho_{\pm} \quad (10)$$

(see Supplementary Materials). For Lévy walks without interactions, one can find $i_{\pm}(x, t) = \int_0^t K(\tau) \rho_{\pm}(x \mp v\tau, t - \tau) d\tau$, where $K(\tau)$ is the memory kernel determined by its Laplace transform [35] $\hat{K}(s) \simeq \frac{1}{T} (1 + As^{\mu-1})$ for $1 < \mu < 2$, as $s \rightarrow 0$ (T is mean running time and A is a constant). For the nonlinear case, the expressions for i_{\pm} are not known. In what follows we use numerical simulations to obtain our results.

Emergence of superdiffusion. To focus on the collective movement and the underlying mechanism of the superdiffusive behaviour of the walkers, we consider non-proliferating walkers ($k(\rho) = 0$) and neglect the repulsion effects ($r \ll a$). Since the turning rate \mathbb{T}_{\pm} , Eq.

(2), depends on both residence time τ and time t (indirectly through ρ_+ and ρ_-), we can not define the running time PDF. It can only be done for the linear case when $f = 1$. For this classical Lévy case the turning rate reads $\mathbb{T}(\tau) = \mu/(\tau_0 + \tau)$ and the running time PDF $\psi(\tau)$ defined in the standard way $\psi(\tau) = \mathbb{T}(\tau) \exp[-\int_0^{\tau} \mathbb{T}(\tau) d\tau]$ [34], becomes the power law density:

$$\psi(\tau) = \frac{\mu \tau_0^{\mu}}{(\tau_0 + \tau)^{1+\mu}}. \quad (11)$$

For $1 < \mu < 2$, this PDF has a finite first moment and infinite second moment. This case corresponds to anomalous subballistic superdiffusion for which the mean squared displacement is $\langle x^2 \rangle \sim t^{3-\mu}$ [6–8].

Importantly, for individuals interacting via alignment we consider $f \neq \text{const.}$ and $\mu > 2$ for which the system without interactions has standard long-time diffusive behaviour: $\langle x^2 \rangle \sim t$ as $t \rightarrow \infty$ (curve (1) in Fig. 2). We do not assume the anomalous running time PDF from the inception as it is done for a classical theory of superdiffusive transport [6–8]. In our simulations we chose $l_a = 1$, $\alpha = 1$ and $\beta = 0$ in Eq. (4), and an exponential interaction function $f(A_{\pm}) = \exp(-A_{\pm})$. For $\alpha = \beta = 1$ we obtain similar results. At $t = 0$ we consider a uniform distribution of individuals in the interval $(-1, 1)$.

Figure 1 illustrates the emergence of the Lévy walk as the ensemble averaged mean squared displacement (MSD) [33] displays superdiffusive behavior (curve (2)). For $\mu = 3$ and $a = 1.5$, we find $\langle (x - x_0)^2 \rangle \simeq t^{1.7}$ (other parameters are listed in the figure caption). Since the individuals disperse in space, their density and therefore the strength of interactions decrease with time. That is, $f \rightarrow 1$ since $A_{\pm} \rightarrow 0$. As the result, the walkers perform a normal diffusion at longer times (curve (2)). Figure 2 confirms the emergence of the Lévy walk. It shows the power law behaviour of the run length PDF with exponent -2.7 for the same parameters used in Fig. 1. A typical trajectory of an individual involves long runs displaying anomalous persistence (walkers collectively move in one direction) (Fig. 3 (b)). The results of our model (Figs. 1, 2) qualitatively explain the emergence of the Lévy walk observed experimentally for swarming bacteria [4]. We show that the standard switching (run-tumble) behaviour of individual is drastically changed due to a collective motion that facilitates the Lévy walk [4]. Interestingly, the alignment interactions lead to the creation of two groups of individuals called clumps that move to the left and to the right (Fig. 3 (a)). This is in agreement with the clumping behaviour observed in non local hyperbolic models for self-organized biological groups [24]. For small interaction strength $a \rightarrow 0$, there is no clumping phenomenon (Fig. 3 (b)).

Nonlinear transition from superdiffusion to diffusion. We now ignore the alignment effects ($f(A_{\pm}) = 1$) and focus on the repulsion/collision interactions. It follows from Eq. (2), the switching rate $\mathbb{T}_{\pm} = \frac{\mu}{\tau_0 + \tau} + \gamma_{\pm}(\rho_{\mp})$, where the interaction term γ_{\pm} is defined in (5). Note that

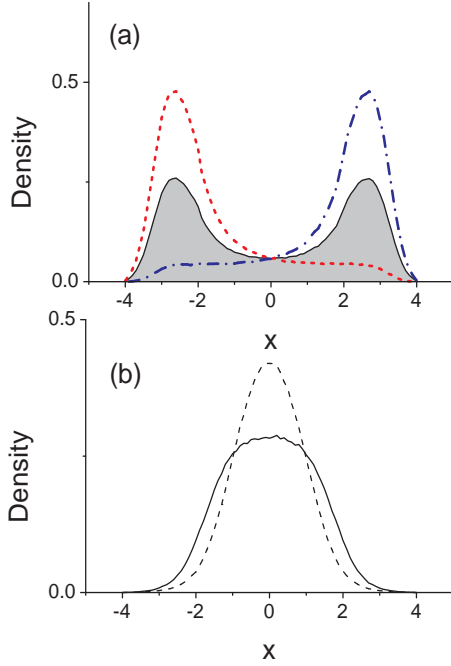


FIG. 3: (a) Alignment leads to the formation of two moving aggregates known as clumps. Density of the walkers ρ (solid curve) develops two bumps corresponding to groups of walkers moving to the left ρ_- (dashed curve) and to the right ρ_+ (dashed-dotted curve). Here $a = 2.5$ and other parameters are the same as in Fig. 2. (b) For weak interactions, $a \rightarrow 0$, we find no Lévy walks and clumping behaviour. The solid curve corresponds to $a = 0.1$. Without interactions the density of walkers (dashed curve) is Gaussian apart from tails. All densities were calculated at $t = 3$.

now we consider the case $1 < \mu < 2$. That is, without interactions we have a subballistic superdiffusive Lévy walk with power law running time density Eq. (11) and the MSD growing as $\langle x^2 \rangle \sim t^{3-\mu}$. We obtain explicit expressions for the total turning rates i_{\pm} in terms of the density of walkers (for the derivation see the Supplementary Materials)

$$i_{\pm}(x, t) = \int_0^t K(t-\tau) \rho_{\pm}(x \mp v(t-\tau), \tau) \times e^{-\int_{\tau}^t \gamma_{\pm}(\rho_{\mp}(x \mp v(t-u), u)) du} d\tau. \quad (12)$$

It is clear from (12) that the rate γ_{\pm} plays the role of a tempering parameter. This term is responsible for the shift of the superdiffusive Lévy walk towards standard diffusion as the density ρ_{\pm} increases. The tempering effect of the repulsion/collision interactions is similar to the tempering due to the random death of walkers [35]. Figure 4 shows the results of numerical simulations corresponding to the rate (2) with $f(A_{\pm}) = 1$. In the absence of repulsion we consider a superdiffusive Lévy walk with $\mu = 1.3$. A typical trajectory (Fig. 4 (b)) has many long runs and the distribution of the run length is a power

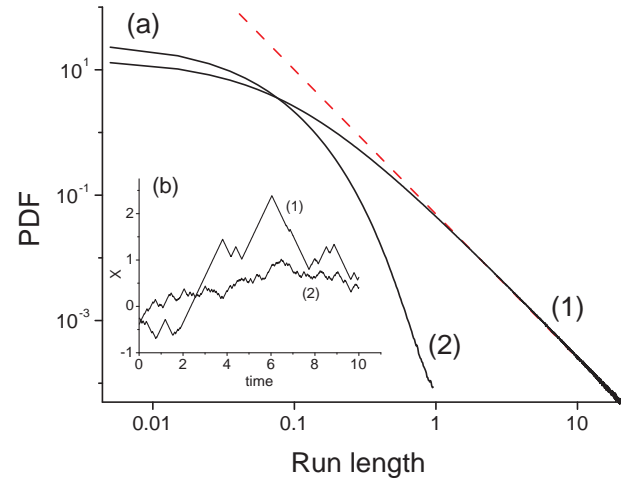


FIG. 4: (a) The run length PDF of individuals interacting repulsively. Interactions lead to the transition to Brownian diffusion. Here we use $r = 10^3$ and $\mu = 1.3$. Other parameters and simulation procedure are the same. The run length PDF transitions from a power law with exponent $-\mu - 1$ for the Lévy walk without interactions (curve (1)) to exponential distribution for the standard diffusion (curve (2)). (b) Typical trajectories of walkers with interactions (curve (2)) and without interactions (curve (1)). Repulsion interactions truncate the long runs of the Lévy walks.

law with exponent $-\mu - 1$ (curve (1) in (a)). Repulsion/collision interactions drastically change the stochastic dynamics of individuals. The long runs are truncated and the trajectory appears Brownian (curve (2) in (b)). The run length PDF becomes exponential (curve (2) in (a)), confirming the transition from a Lévy walk to Brownian diffusion. Such a transition was observed experimentally in the movement of mussels as their density increases [5].

Summary. We have proposed a nonlinear persistent random walk model of collectively moving individuals that interact via alignment and repulsion. The walkers' interactions have been taken into account on the mesoscopic level, at which the individuals' turning rate depends on the mean field population density (nonlinear effect) and running time since the last velocity switching (non-Markovian effect). The main result of this paper is that the non-local alignment leads to the anomalous nonlinear persistence of the random walkers and the emergence of the Lévy walk as a collective phenomenon. Importantly this emergent superdiffusive movement of individuals is a nonlinear non-Markovian effect, and is not based on the standard assumption of a power-law running time distribution from the inception. We should note that non-Markovian effects are crucial, since the numerical simulations of the nonlinear model without the running time dependence in (2) show no Lévy walks. We have qualitatively explained (1) the experimentally observed emergence of superdiffusive Lévy

walks of swarming bacteria due to their collective dynamics and (2) the transition from subballistic superdiffusion to the Brownian motion of individuals interacting via repulsion/collision, which was observed in the movement of mussels as their density increases. Our results are relevant to experimentally observed superdiffusion of micron-scale beads in bacterial bath [36], where it has been found that the superdiffusion occurs as a result of the collective

dynamics due to formations of coherent structures like jets. Potentially, our model could be useful for studying collective behavior of interacting individuals such as bacteria which use collective movement for better protection against multiple antibiotics [37].

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I. SUPPLEMENTARY MATERIALS

A. 2-D generalization of nonlinear Lévy walk model

In 2-D we consider the random motion of an individual that runs in the direction $\theta = (\cos \varphi, \sin \varphi)$ with the constant velocity v during the running time τ , and changes the direction at (\mathbf{x}, t) to $\theta' = (\cos \varphi', \sin \varphi')$. The turning rate $\mathbb{T}_\rho(\mathbf{x}, t, \tau, \varphi, \varphi')$ from φ to φ' at (\mathbf{x}, t) depends on the running time τ and the non-local interactions with neighboring conspecifics. We define the mean structural density of individuals, $n(\mathbf{x}, t, \tau, \varphi)$, at point \mathbf{x} and time t moving in the direction θ and having started the move a time τ ago. The governing equation for $n(\mathbf{x}, t, \tau, \varphi)$ takes the form [30]

$$\frac{\partial n}{\partial t} + v\theta \cdot \nabla n + \frac{\partial n}{\partial \tau} = -\gamma_\rho(\mathbf{x}, t, \tau, \varphi) n, \quad (13)$$

where γ_ρ can be defined in terms of the turning rate \mathbb{T}_ρ as follows

$$\gamma_\rho(\mathbf{x}, t, \tau, \varphi) = \int_{-\pi}^{\pi} \mathbb{T}_\rho(\mathbf{x}, t, \tau, \varphi, \varphi') d\varphi'. \quad (14)$$

The function $\gamma_\rho(\mathbf{x}, t, \tau, \varphi)$ describes the rate at which the individual changes the direction at (\mathbf{x}, t) from φ to other directions due to interactions with neighboring conspecifics. We assume that at the initial time $t = 0$ all individuals have zero running time

$$n(\mathbf{x}, 0, \tau, \varphi) = \rho(\mathbf{x}, 0, \varphi) \delta(\tau). \quad (15)$$

The total population density is

$$\rho(\mathbf{x}, t, \varphi) = \int_0^t n(\mathbf{x}, t, \tau, \varphi) d\tau. \quad (16)$$

We set up the boundary condition at zero running time $\tau = 0$:

$$n(\mathbf{x}, t, 0, \varphi) = \int_0^t \int_{-\pi}^{\pi} \mathbb{T}_\rho(\mathbf{x}, t, \tau, \varphi', \varphi) n(\mathbf{x}, t, \tau, \varphi') d\varphi' d\tau. \quad (17)$$

From the Markovian equation (13) together with (15) and (17) one can obtain the equation for $\rho(\mathbf{x}, t, \varphi)$ [15]

$$\frac{\partial \rho}{\partial t} + v\theta \cdot \nabla \rho = -i(\mathbf{x}, t, \varphi) + n(\mathbf{x}, t, 0, \varphi), \quad (18)$$

where

$$i(\mathbf{x}, t, \varphi) = \int_0^t \gamma_\rho(\mathbf{x}, t, \tau, \varphi) n(\mathbf{x}, t, \tau, \varphi) d\tau. \quad (19)$$

In the linear case without interactions, one can find $i(\mathbf{x}, t, \varphi)$ in terms of the total density $\rho(\mathbf{x}, t, \varphi)$ [15]

$$i(\mathbf{x}, t, \varphi) = \int_0^t K(t - \tau) \rho(\mathbf{x} - v\theta(t - \tau), \tau, \varphi) d\tau, \quad (20)$$

where $K(t)$ is the standard memory kernel [14].

Non-local interactions involving alignment rate \mathbb{T}_{al} and repulsion/collision rate \mathbb{T}_r can be modelled as follows:

$$\mathbb{T}_\rho = \mathbb{T}_{al} + \mathbb{T}_r, \quad (21)$$

where

$$\mathbb{T}_{al} = \frac{\mu}{\tau_0 + \tau} \int_{-\pi}^{\pi} \int_{\mathbb{R}^2} K_{al}^d(\mathbf{x} - \mathbf{y}) K_{al}^o(\chi, \varphi') \times \omega_{al}(\varphi' - \varphi, \varphi' - \chi) \rho(\mathbf{y}, t, \chi) d\mathbf{y} d\chi, \quad (22)$$

$$\mathbb{T}_r = r(\tau) \int_{-\pi}^{\pi} \int_{\mathbb{R}^2} K_r^d(\mathbf{x} - \mathbf{y}) K_r^o(\mathbf{x}, \mathbf{y}, \varphi') \times \omega_r(\varphi' - \varphi, \varphi' - \psi) \rho(\mathbf{y}, t, \chi) d\mathbf{y} d\chi. \quad (23)$$

The explicit expressions for the functions $K_{al,r}^d$, $K_{al,r}^o$ and $\omega_{al,r}$ can be found in [25, 26]. Detailed study of 2-D model will follow.

B. Equations for the unstructured densities $\rho_\pm(x, t)$

Balance equations for the unstructured densities can be found by differentiating

$$\rho_\pm(x, t) = \int_0^t n_\pm(x, t, \tau) d\tau \quad (24)$$

with respect to time t . Because of the initial condition

$$n_\pm(x, 0, \tau) = \frac{\rho(x, 0)}{2} \delta(\tau), \quad (25)$$

the running time τ varies from 0 to t . We obtain for ρ_\pm the following equation

$$\begin{aligned} \frac{\partial \rho_\pm}{\partial t} &= n_\pm(x, t, t) \mp v \int_0^t \frac{\partial n_\pm}{\partial x} d\tau - \int_0^t \frac{\partial n_\pm}{\partial \tau} d\tau \\ &\quad - \int_0^t \mathbb{T}_\pm(\tau, \rho_+, \rho_-) n_\pm d\tau. \end{aligned}$$

Since a zero running time condition ($\tau = 0$) involves the proliferation of the individuals with the proliferation rate $k(\rho)$:

$$n_\pm(x, t, 0) = \int_0^t [\mathbb{T}_\mp(\tau, \rho_+, \rho_-) n_\mp + k(\rho) n_\pm] d\tau, \quad (26)$$

we rewrite the equation for $\frac{\partial \rho_\pm}{\partial t}$ as follows

$$\frac{\partial \rho_\pm}{\partial t} \pm v \frac{\partial \rho_\pm}{\partial x} = i_\mp(x, t) - i_\pm(x, t) + k(\rho) \rho_\pm, \quad (27)$$

where

$$i_\pm(x, t) = \int_0^t \mathbb{T}_\pm(\tau, \rho_+, \rho_-) n_\pm(x, t, \tau) d\tau. \quad (28)$$

C. Nonlinear transition from superdiffusion to diffusion.

Now let us find the switching rate $i_{\pm}(x, t)$ in terms of the density $\rho_{\pm}(x, t)$ for the rate

$$\mathbb{T}_{\pm}(\tau, \rho_+, \rho_-) = \frac{\mu}{\tau_0 + \tau} + \gamma_{\pm}(\rho_{\mp}). \quad (29)$$

The purpose is show that γ_{\pm} plays the role of nonlinear tempering. By using the method of characteristics we solve the equation

$$\frac{\partial n_{\pm}}{\partial t} \pm v \frac{\partial n_{\pm}}{\partial x} + \frac{\partial n_{\pm}}{\partial \tau} = -\mathbb{T}_{\pm}(\tau, \rho_+, \rho_-) n_{\pm}. \quad (30)$$

We find for $\tau < t$

$$n_{\pm}(x, t, \tau) = n_{\pm}(x \mp v\tau, t - \tau, 0) \times \Psi(\tau) e^{-\int_{t-\tau}^t \gamma_{\pm}(\rho_{\mp}(x \mp v(t-u), u)) du}. \quad (31)$$

where the survival function $\Psi(\tau)$ is

$$\Psi(\tau) = \left(\frac{\tau_0}{\tau_0 + \tau} \right)^{\mu}. \quad (32)$$

The formula (31) can be rewritten as

$$n_{\pm}(x, t, \tau) = n_{\pm}(x \mp v\tau, t - \tau, 0) \Psi(\tau) \frac{F_{\rho}(x, t)}{F_{\rho}(x, \tau)} \quad (33)$$

where

$$F_{\rho}(x, t) = e^{-\int_0^t \gamma_{\pm}(\rho_{\mp}(x \mp v(t-u), u)) du}. \quad (34)$$

Taking into account the initial condition (25) and substituting (33) into we obtain

$$i_{\pm}(x, t) = \int_0^t n_{\pm}(x \mp v\tau, t - \tau, 0) \psi(\tau) \frac{F_{\rho}(x, t)}{F_{\rho}(x, \tau)} d\tau + \frac{1}{2} \rho(x \mp vt, 0) \psi(t) F_{\rho}(x, t) \quad (35)$$

and

$$\rho_{\pm}(x, t) = \int_0^t n_{\pm}(x \mp v\tau, t - \tau, 0) \Psi(\tau) \frac{F_{\rho}(x, t)}{F_{\rho}(x, \tau)} d\tau + \frac{1}{2} \Psi(t) \rho(x \mp vt, 0) F_{\rho}(x, t). \quad (36)$$

where $\psi(\tau) = -d\Psi(\tau)/d\tau$. By using the Laplace transforms one can eliminate $n_{\pm}(x, t, 0)$ from the above equations and obtain explicit expressions for the total turning rates i_{\pm} in terms of the density of walkers ρ_{\pm} :

$$i_{\pm}(x, t) = \int_0^t K(t - \tau) \rho_{\pm}(x \mp v(t - \tau), \tau) \times e^{-\int_{\tau}^t \gamma_{\pm}(\rho_{\mp}(x \mp v(t-u), u)) du} d\tau. \quad (37)$$

This term involves the exponential factor in which the rate γ_{\pm} plays the role of a tempering parameter. This rate leads to the shift of the superdiffusive Lévy walk towards Brownian motion as the density ρ_{\pm} increases. The main feature of the rate $i_{\pm}(x, t)$ is that although the rates $\frac{\mu}{\tau_0 + \tau}$ and $\gamma_{\pm}(\rho_{\mp})$ are additive (see (29)), the corresponding terms in the rate (37) are not additive. This is clearly a non-Markovian tempering effect.